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EFFECTS OF SALINITY AND TEMPERATURE ON THE PREDATION RATE OF *THAIS HAEMASTOMA* ON *CRASSOSTREA VIRGINICA* SPAT

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Metabolism and activity of aquatic invertebrates are influenced by environmental factors. In the estuarine habitat, two important factors are temperature and salinity (Kinne, 1971). To a great extent, the interaction and fluctuation of these two factors regulate the activity and distribution of estuarine invertebrates. Kinne (1971) has stressed the importance of multifactorial experiments involving the effects of salinity and temperature upon estuarine invertebrates.

Previous studies have been conducted on the southern oyster drill, *Thais haemastoma,* which is a serious predator of the commercial oyster, *Crassostrea virginica.* Aspects of predation and estuarine distribution of *T. haemastoma* have been described (Burkenroad, 1931; St. Amant, 1938, 1957; Butler, 1953; and Belisle and Stickle, 1978). St. Amant (1938, 1957) reported that *T. haemastoma* is unable to penetrate estuaries below salinities of 15‰, although later laboratory work (Stickle and Howey, 1975) indicated that drills can tolerate salinities of 5‰ at 20° C for at least 10 days. Below 12° C, *T. haemastoma* becomes torpid and inactive (St. Amant, 1957).

The effects of temperature and salinity on the rates of predation by other, closely related species, *Urosalpinx cinerea, Eupleura caudata* and *Thais lapillus,* have been investigated (Hanks, 1957; Manzi, 1970a, b; Zachary and Haven, 1973; and Bayne and Scullard, 1978). Using *Crassostrea virginica* spat and *Mytilus edulis* as prey, Manzi (1970a) demonstrated that the predation rates of *U. cinerea* and *E. caudata* increased with temperature and salinity. Maximum predation rates were observed at the highest temperature and salinity combination used, 26‰ salinity at 25° C. Zachary and Haven (1973) found the activity of *U. cinerea* to increase with salinity. However, drills exposed to fluctuating salinity regimes exhibited lower levels of activity and survival than those under constant salinity. In these trials, the magnitude of the salinity fluctuations was an important factor affecting drill activity and survival (Zachary and Haven, 1973). The predation rate of *Thais lapillus,* preying on *M. edulis,* is temperature-sensitive and shows seasonal variability (Bayne and Scullard, 1978).

The purpose of this investigation was to determine the effect of temperature and salinity interactions on the predation rate of *T. haemastoma* on spat of *C. virginica.* To more accurately reflect the estuarine conditions to which drills are frequently exposed, the effects of simulated tidal fluctuations of salinity on the predation rate of the oyster drill were also studied.

Materials and Methods

Oyster drills

Specimens of *T. haemastoma* were collected during the summer and fall of 1977, and early spring of 1978, from the vicinity of Caminada Pass near Grand Isle,

Louisiana, U. S. A. Drills were placed in 38-liter aquaria at room temperature (22°–25° C) and field salinity (Instant Ocean sea water mix). Salinity was adjusted 2‰ per day until the desired salinity was attained. The drills were then allowed to acclimate at constant salinity for at least one week prior to temperature adjustment. Snails were transferred from room temperature, and the water temperature was allowed to change gradually to the experimental temperature over a period of about 8 hr. Drills were acclimated for at least 10 days at constant temperature and salinity prior to the start of the experiment. For 20° and 30° C experiments, the aquaria were placed in a large temperature-controlled water bath. An environmental chamber was used for the 10° C and low-temperature threshold experiments. The drills were under normal light intensity from ceiling illumination and there did not appear to be any phototactic response by the drills.

Oyster spat

Cultured, cultchless *C. virginica* spat were used as prey. Spat averaged approximately 2 to 3 cm in length and 0.8 to 1.0 g total weight. Spat size and weight varied with season, but were uniform within shipments. During the summer of 1977, spat were supplied by the oyster hatchery operated by the Gulf Coast Research Laboratory at Ocean Springs, Mississippi. The Horn Point Environmental Laboratory operated by the University of Maryland at Cambridge, Maryland, supplied spat during the fall of 1977 and summer of 1978. Upon arrival, the spat were placed in holding aquaria at room temperature and at constant salinities of 15‰ and 25‰. Spat at 15‰ were directly transferred to 7.5, 10.0, 15.0 and 20‰ experimental aquaria and spat at 25‰ were transferred to 20, 30, and 35‰ experimental aquaria. The use of cultured, cultchless oyster spat insured uniform prey size and equal caloric value for each prey item consumed. Dame (1972) found no significant seasonal variation in the caloric content of small (<20 g whole weight) intertidal oysters.

Feeding rate determinations

To determine the individual feeding rates, a drill was placed in each of 8 compartments formed by dividing 38-liter aquaria with slotted plexiglass panels. Oyster drills of uniform length (~45 mm) were selected to remove size as a variable within experimental design. The feeding rate was determined by removing and counting the number of spat consumed each day. A density of 5 spat per drill was maintained throughout the experiment. By weighing the spat beforehand and the empty valves afterwards the total wet weight of oyster flesh consumed over the course of the experiment was determined. Per cent body water was determined by exposing a group of spat to each temperature and salinity combination. Per cent body water was measured as: (total wet wt. minus total dry wt.) times 100, divided by the total wet wt. The per cent body water was used to convert total wet weight of oyster flesh consumed to a dry weight basis. The predation rate was measured as the average daily feeding rate (ADFR, spat per drill/day) and the ingestion rate as grams dry weight (DW) consumed per drill during the 21-day experiment. The initial and final length and weight, and the sex of each drill were recorded.

The drills were provided with adult specimens of *C. virginica* during acclimation until 1 week prior to the start of the experiment. At that time the drills

were provided with oyster spat. Following acclimation and conditioning, the predation rate was measured daily for 21 days.

Salinity and temperature regimes

Feeding rates were determined at steady state salinities of 7.5, 10, 15, 20, 25, 30 and 35‰ at 10°, 20° and 30° C. The 20° C experiment was performed in August, 1977, the 10° C experiment in November, 1977, and the 30° C experiment in July, 1978. The 35‰ treatment at 20° C was omitted.

Oyster drills were exposed to simulated diurnal salinity fluctuation patterns of 30 to 10 to 30‰ and 10 to 30 to 10‰ at 10°, 20° and 30° C, using procedures similar to those given by Stickle and Ahokas (1974). During diurnal cycles, salinity was increased or decreased over a 10-hr period, held at slack water for 2 hr, changed in the opposite direction over 10 hr and held at the initial salinity for 2 hr. These cycles ran continuously for 21 days. Each salinity fluctuation regime was duplicated.

Temperature threshold and group versus individual experiments

The low temperature threshold at which drills begin to prey on oyster spat was evaluated. The predation rate of drills at salinities of 20‰ was determined for temperatures of 12.5°, 15.0° and 17.5° C.

Finally, individual feeding rates were compared with those of a group at 25° C and 20‰. This experiment was carried out in order to test the hypothesis that drills that are more efficient at killing oysters may provide food for scavenging conspecifics. Because oyster spat were too small to permit aggregate feeding, adult oysters were used in this experiment. Both the temperature threshold and the group *vs.* individual predation rate experiments were performed in July, 1978.

Statistical analyses

Two-way analysis of variance was performed using the general linear model method on the data from the 20° and 30° C experiments (Statistical Analysis System, Barr, Goodnight, Sall and Helwig, 1976). The two variables analyzed were dry weight of oyster flesh consumed during the trial and the average daily feeding rate. The general linear model included salinity, temperature and sex, plus all four possible interactions and was corrected for drill length and weight differences in each cell. Duncan's multiple range test was used to determine significant differences of means of the two variables within each temperature treatment. This test was also used to compare means in the low temperature threshold experiment. A *t*-test was used for the group versus individual feeding rate trial. Statistical significance is given at the $P < 0.05$ level.

Results

The average daily feeding rate (ADFR) and dry weight of oyster flesh consumed (DW) were highly correlated in all experiments ($r = 0.925$). These two variables are equal indicators of predation.

Statistical analysis of the data for the temperature threshold, and the 20° and 30° C experiments do not indicate significant ($P > 0.05$) relationships between predation rate and drill total weight or length. Likewise, 2-way analysis of vari-

Table I

Results of the temperature threshold experiment. ADFR = average daily feeding rate; DW = g dry weight of oyster flesh consumed in 21 days. Values are means ± standard error. Salinity was 20‰; N = 8 for each temperature.

Temperature (°C)	ADFR	DW
12.5	0.119 ± 0.018	0.254 ± 0.049
15.0	0.875 ± 0.111	1.625 ± 0.216
17.5	1.387 ± 0.086	2.341 ± 0.123

ance for the 20° and 30° C experiments reveals no significant effects related to sex. Therefore, both sexes were combined in the statistical model.

Mortality and egg capsule deposition

Mortality during the period of acclimation for the 20° and 30° C trials, the temperature-dependent feeding threshold experiment, and the group versus individual feeding rate trial was less than five per cent. No mortality was observed during any of the experimental periods in these experiments. In the 10° C trial, 7 out of 78 snails died during the last 2 weeks of the experiment. Three drills died at both 30 and 35‰ and one drill died in the 30 to 10 to 30‰ cycle. These drills were not replaced.

Egg capsule deposition was observed among the snails collected in the early spring of 1978. These snails were used for the 30° C trial, the temperature threshold experiment and the group vs. individual feeding experiments. Prolific capsule deposition lasted approximately 6 weeks during the period of acclimation at the constant acclimation salinities of 15, 20 and 25‰ at 30° C and 20‰ at room temperature (approximately 25° C). No capsule deposition occurred during the 21-day experimental period.

Temperature and salinity interactions

The temperature threshold for predation was between 10° and 12.5° C and a temperature-dependent relationship of predation rate exists between 12.5° and 17.5° C (Table I). Predation and ingestion rates in the temperature threshold experiment were significantly different at each temperature as revealed by Duncan's multiple range test.

Although sporadic predation was observed at 10° C, the predation rate was effectively 0 (Fig. 1). During the 21-day trial; 2 spat were consumed by 8 drills at 15‰, 3 spat at 20‰ and 1 spat at 25‰ and the 10 to 30 to 10‰ cycle. No spat were consumed in the other salinity treatments. The drills remained attached to the substrate during the experiment, but were in a "torpid" state and showed very little movement.

Duncan's multiple range tests performed on predation and ingestion rate means at 20° C show that both ADFR and DW were significantly greater for drills at salinities of 15‰ than for drills at 7.5‰ and 10 to 30 to 10‰ (Fig. 1). At 7.5‰, the predation rate was significantly less than those observed between 10 and 25‰. Predation rates at 10, 15, 20, 25 and 30‰ and in the 2 fluctuating cycles were not significantly different.

At 30° C, the 7.5‰ ADFR was significantly less than ADFRs for all other

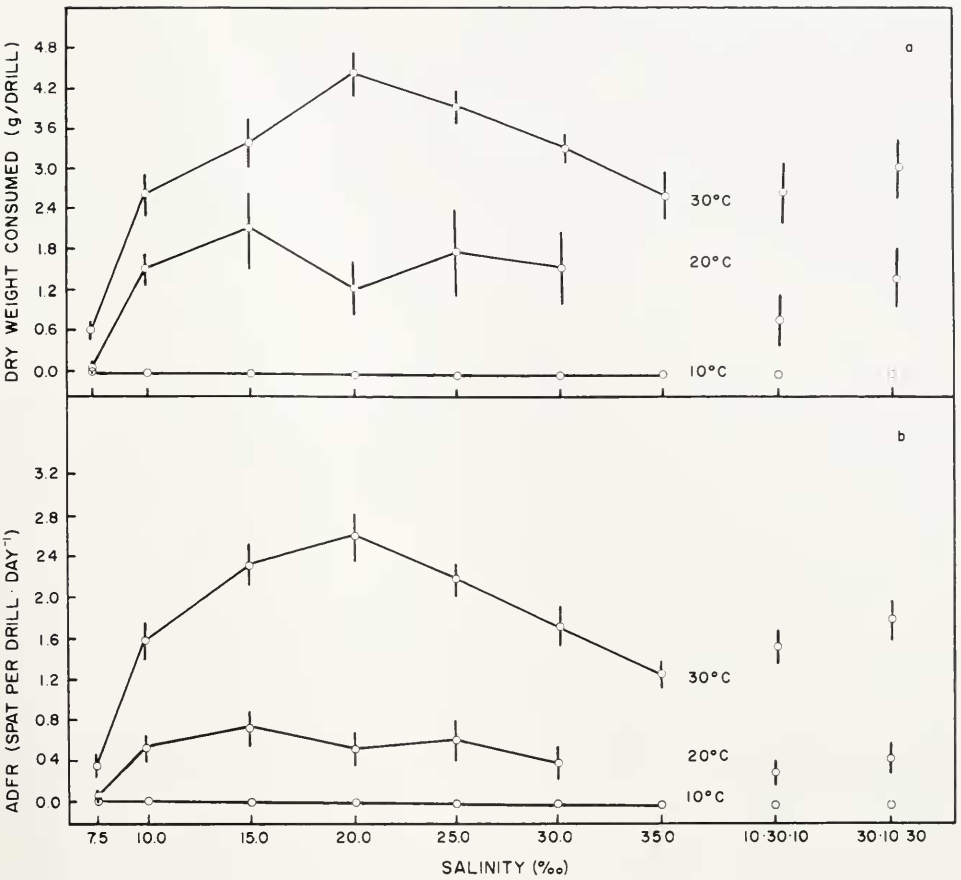

FIGURE 1. Ingestion rate of *Thais haemastoma*, expressed as g dry weight of oyster flesh consumed during 21 days, a, and predation rates as the average daily feeding rate, b. The ingestion and predation rates are presented as means (symbol) ± 1 standard error (vertical bar).

salinities, while the 20‰ ADFR was significantly greater than the predation rates at all other salinities (Fig. 1). The predation rates at salinities of 15 and 25‰ were significantly greater than the ADFRs for 10, 30 and 35‰ and the two fluctuating salinity cycles. The predation rates in the latter five salinity treatments were not significantly different. The means for ingestion rate reveal slightly different results than the ADFR. Dry weight consumption at 20‰ was significantly greater than at all other salinities except 25‰. Dry weight consumption at 35‰ was significantly less than consumption at 30‰ and during the 30 to 10 to 30‰ fluctuating salinity cycle.

Overall, there was a significant interaction of salinity and temperature effects upon predation rates. The effect of constant salinity on predation rates at 20° C was not as pronounced as at 30° C (Fig. 1). There was no change in predation or ingestion rates above 20‰ at 20° C, while there was a significant decrease in predation rates above 20‰ at 30° C. However, there was no significant interaction between salinity cycle (*i.e.* 10 to 30 to 10‰ *vs.* 30 to 10 to 30‰) and temperature effects upon predation rates.

Group vs. individual predation rates

During the 17 days of this experiment, drills consumed 20 large oysters in the divided aquarium and 21 oysters in the undivided, or group, aquarium. The total consumption of oysters by snails in the divided aquarium was 10.5 ± 1.0 g dry weight per drill and 11.7 ± 0.1 g dry weight in the undivided aquarium. No significant difference in consumption of oyster flesh existed between the two groups. The predation rate for the group was 0.13 oysters/(drill·day) while the individual drills consumed 0.12 oysters/(drill·day). Large oyster entire weight averaged 234 g.

Discussion

Predation by *Thais haemastoma* upon oyster spat is affected by salinity and temperature. The effect of constant salinity treatments on the predation rate differs with temperature. At 20° C consant salinity treatments between 10 and 30‰ did not influence predation rates. At 30° C, there is a narrow optimum for predation at 20‰, above which the predation rates decrease. Manzi (1970a) also reported that temperature and salinity interact, affecting the predation rates of *Urosalpinx cinerea* and *Eupleura caudata*.

Previous studies have shown that the response of estuarine organisms to chronic salinity stress or acute salinity stress (direct transfer experiments) are different from natural tidal fluctuations of salinity (Stickle and Ahokas, 1974; Stickle and Howey, 1975; Findley, Belisle, and Stickle, 1978). Predation rates of *T. haemastoma* in 10 to 30 to 10‰ and 30 to 10 to 30‰ fluctuating salinity cycles are not significantly different. Therefore, the initial acclimation to constant salinity prior to starting the salinity cycles does not affect the predation rates. Furthermore, the predation rates in these fluctuating salinity cycles are not significantly different from those in the constant acclimation salinities of 10 and 30‰ at each respective temperature. This is evidence of functional euryhalinity in *T. haemastoma*. Tidal fluctuations of this magnitude occur infrequently and are considered near the maximum naturally occurring salinity fluctuations, yet are compatible with *T. haemastoma* feeding and survival.

The low temperature limit for predation in *T. haemastoma* from the Gulf of Mexico is slightly higher than that for a closely related species from the North Atlantic coast, *Urosalpinx cinerea*. Specimens of *U. cinerea* collected from Long Island Sound began feeding between 5° and 10° C at 25‰ (Hanks, 1957). The feeding rate increased until the temperature reached 25° C and then declined at 30° C. *T. haemastoma* fed sporadically below 12.5° C and at its maximum rate at 30° C, the upper temperature investigated in this experiment. These differences in response to temperature are thought to be a result of the geographic distribution of the two species. *T. haemastoma* has a more southerly distribution, and is therefore exposed to higher temperatures than *U. cinerea*.

Thais haemastoma also displayed a greater tolerance to salinity stress than *Urosalpinx cinerea* and *Eupleura caudata*. The minimum salinity compatible with predation by the latter two species was 12.5‰ at 15°, 20° and 25° C (Manzi, 1970a). In this study, *T. haemastoma* fed lightly at 7.5‰ and 20° and 30° C. In a preliminary study to determine lower lethal limits, adult specimens of *T. haemastoma* tolerated 5‰ at room temperature (approximately 25° C) for 1 month without mortality, although the snails appeared swollen and did not feed.

These results indicate that *T. haemastoma* is a euryhaline organism with ex-

treme tolerance to salinity stress. Previous published data have demonstrated this species to be an osmoconformer and to physiologically respond to changes in salinity in a manner similar to stenohaline organisms. Oxygen consumption in *T. haemastoma* decreases when the salinity is fluctuated upward or downward from the acclimation salinity, a characteristic of stenohaline organisms (Findley *et al.,* 1978). This species also displays little ion or volume regulation. In fluctuating salinities, hemolymph composition and osmolality track ambient sea water (Stickle and Howey, 1975).

Although *T. haemastoma* can prey on oyster spat over a wide range of temperatures and salinities, an understanding of its energy budget balance is lacking. However, the energy budget for a related muricid gastropod, *Thais lapillus,* varies as a function of temperature and season (Bayne and Scullard, 1978). The "scope for growth," the number of calories remaining after the metabolic demands of the individual were met, was greater for specimens of *T. lapillus* collected in the fall (16° C) than for drills collected in the spring (9° C). Since prey selection was assumed not to vary seasonally, the difference was primarily due to changes in predation rate and oxygen consumption (Bayne and Scullard, 1978). The estuarine environment is typified by such seasonal variations in salinity and temperature, similar to those explored in this experiment with *T. haemastoma.* The predation rate and oxygen consumption of the southern oyster drill varies with temperature and salinity and future experiments are planned to determine if the scope for growth also changes for this species.

Field observations indicate that *T. haemastoma* is rarely found in estuarine regions where the average salinity is less than 15‰ (St. Amant, 1938). If adult drills are tolerant of salinity stress, why are they excluded from estuarine regions of less than 15‰? There is limited evidence for speculating that reproduction and larval development are the critical points of the life cycle that are sensitive to reduced salinity. Capsule deposition in the laboratory at 30° C did not occur below 15‰ and Wells (1961) reported that larval specimens of *T. haemastoma* did not survive the 5-day test period below 10‰. It appears that if some larvae did invade the upper limit of an estuary during low river discharge (elevated salinity) and mature, they would fail to form a breeding population. Exposed to chronic low salinities, less than 15‰, their predation rates would be greatly reduced. Isolated populations would be difficult to detect because *T. haemastoma* does not always bore through oyster valves, therefore they leave little permanent evidence of predation (McGraw and Gunter, 1972).

In the laboratory, specimens of *T. haemastoma* characteristically feed in aggregates on adult specimens of *C. virginica.* Although it is possible that group feeding by drills would exceed the total rate for individual drills, this was not the case in our study. Individual snails, averaging 52.6 mm in length, were as capable of killing and feeding on adult oysters as members of a feeding aggregation.

T. haemastoma possesses a paralytic venom that causes oysters to gape, exposing the oyster tissue. In specimens of *T. haemastoma* from Italy, Roseghini (1971) found dihydromurexine from hypobranchial gland extracts. Whittaker (1960) found senecioylcholine in the hypobranchial gland of *T. floridana* (= *T. h. floridana*) from Florida. Both of these compounds function as powerful neuromuscular blocking agents. This paralytic capability may partially explain why *T. haemastoma* is able to prey over a wide range of salinities. No preference for drilling or envenomation was noted at any salinity or temperature during this experiment. However, the use of fairly small spat made such a determination difficult.

The energy expenditures required for either method of attack are totally unknown, but *T. haemastoma* has an advantage in possessing a typical muricid radular apparatus and accessory boring organ (See Carriker, 1978) as well as a venom.

Because *T. haemastoma* tolerates ambient salinity well below its distributional limit in estuaries and it also maintains high predation rates below the 15‰ limit suggested by field observations (St. Amant, 1938, 1957), other physiological factors may cause stress in the southern oyster drill. Indexes of physiological stress have recently been developed with other molluscs which may aid in explaining the disparity between the field distribution of the species and laboratory observations of its metabolism and activity as related to salinity. These indexes include scope for growth, growth efficiency and oxygen : nitrogen (O : N) ratios (Bayne and Scullard, 1978; Widdows, 1978). These stress indexes are currently being applied to *T. haemastoma* as a function of temperature and salinity.

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Summary

1. The predation and ingestion rate of *Thais haemastoma* on oyster spat is sensitive to temperature and salinity. The effect of salinity on predation rate was different at 20° and 30° C.

2. The temperature threshold for predation was between 10° and 12.5° C; drills were not observed to feed below 7.5‰.

3. Drills exposed to diurnal tidal fluctuations of salinity, reflecting the estuarine environment, had predation rates significantly less than those at the optimal constant salinity (20‰) at 30° C, but were not significantly less at 20° C. The predation and ingestion rates in the fluctuating salinity cycles were not significantly different than rates for drills at the constant acclimation salinities of 10 and 30‰.

4. Predation rates were not significantly affected by drill sex or weight and length. However, the experiments were designed to exclude size effects by selecting drills within a size range of 45 to 55 mm.

5. Predation rates were not significantly different between large drills feeding as individuals (1 drill/adult oyster) or as aggregates (>1 drill/adult oyster).

6. The predation and ingestion rate data indicate a functional euryhalinity in *T. haemastoma*. This species of oyster drill can tolerate changes in its physiology accompanying changes in temperature and salinity and still maintain its ability to function as an efficient predator.

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